Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques?

Lehner, S R ; Burkart, J M ; van Schaik, C P

Abstract: While striking cultural variation in behavior from one site to another has been described in chimpanzees and orangutans, cumulative culture might be unique to humans. Captive chimpanzees were recently found to be rather conservative, sticking to the technique they had mastered, even after more effective alternatives were demonstrated. Behavioral flexibility in problem solving, in the sense of acquiring new solutions after having learned another one earlier, is a vital prerequisite for cumulative build-up of techniques. Here, we experimentally investigate whether captive orangutans show such flexibility, and if so, whether they show techniques that cumulatively build up (ratchet) on previous ones after conditions of the task are changed. We provided nine Sumatran orangutans (Pongo pygmaeus abelii) with two types of transparent tubes partly filled with syrup, along with potential tools such as sticks, twigs, wood wool and paper. In the first phase, the orangutans could reach inside the tubes with their hands (Regular Condition), but in the following phase, tubes had been made too narrow for their hands to fit in (Restricted Condition 1), or in addition the setup lacked their favorite materials (Restricted Condition 2). The orangutans showed high behavioral flexibility, applying nine different techniques under the regular condition in total. Individuals abandoned preferred techniques and switched to different techniques under restricted conditions when this was advantageous. We show for two of these techniques how they cumulatively built up on earlier ones. This suggests that the near-absence of cumulative culture in wild orangutans is not due to a lack of flexibility when existing solutions to tasks are made impossible.

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Can captive orangutans (*Pongo pygmaeus abelii*) be coaxed into cumulative build-up of techniques?

Stephan R. Lehner, Judith M. Burkart, Carel P. van Schaik
University of Zurich

Author Note

Stephan R. Lehner, Judith M. Burkart, Carel P. van Schaik, Anthropological Institute and Museum, University of Zurich

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Correspondence concerning this article should be addressed to Stephan R. Lehner, Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland. E-mail: slehner@aim.uzh.ch

Abstract

While striking cultural variation in behavior from one site to another has been described in chimpanzees and orangutans, cumulative culture seems to be far more pronounced in humans. Captive chimpanzees were recently found to be rather conservative, sticking to the technique they had mastered, even after more effective alternatives were demonstrated. Behavioral flexibility in problem solving, in the sense of acquiring new solutions after having learned another one earlier, is a vital prerequisite for cumulative build-up of techniques. Here, we experimentally investigate whether captive orangutans show such flexibility, and if so, whether they show techniques that cumulatively build up (ratchet) on previous ones after conditions of the task are changed. We provided nine Sumatran orangutans with two types of transparent tubes partly filled with syrup, along with potential tools such as sticks, twigs, wood wool and paper. In the first phase, the orangutans could reach inside the tubes with their hands (regular condition), but in the following phase, tubes had been made too narrow for their hands to fit in (restricted condition 1), or in addition lacked their favorite materials (restricted condition 2). The orangutans showed high behavioral flexibility, applying nine different techniques under the regular condition, abandoning preferred techniques and switching to different techniques under restricted conditions when this was advantageous. Two of these techniques cumulatively built up on earlier ones. This suggests that the near-absence of cumulative culture in wild orangutans is not due to a lack of flexibility when existing solutions to tasks are made impossible.

Keywords: behavioral flexibility, cumulative build-up, cumulative culture, ratcheting, orangutan

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Introduction

For a long time, culture was considered unique to our own species and therefore inaccessible to analysis by the comparative method (Byrne, 2007). But recently, based on extensive fieldwork, striking behavioral variations from one site to another have been described to constitute culture in our closest living relatives, chimpanzees (Boesch, 1996; Whiten et al., 1999) and orangutans (van Schaik et al., 2003).

Human cultural traditions change over time, and many seem to accumulate modifications made by different individuals over time in the direction of greater complexity, a phenomenon called cumulative cultural evolution or ratcheting (Tomasello, Kruger, & Ratner, 1993). Greater complexity means that a wider range of functions is encompassed (Boesch & Tomasello, 1998). Such modifications have often been understood to represent improvements (Marshall-Pescini & Whiten, 2008; Tennie, Call, & Tomasello, 2009), be more efficient or productive (Laland, 2004; Marshall-Pescini & Whiten, 2008), or be an elaboration of a previous one (Marshall-Pescini & Whiten, 2008). Some have argued that cumulative cultural evolution is limited to humans (Henrich & McElreath, 2003; Tomasello, 2001; Tomasello et al., 1993). Others think it is limited to humans, song birds, and perhaps chimpanzees (Boyd & Richerson, 1996). Indeed, Whiten et al. (2003) and Boesch (2003) argued that there are examples which show that chimpanzees do have some modest power for cumulative build-up of techniques. For instance, many chimpanzee populations crack nuts by hitting them directly with the hand against tree trunks or are using stone hammers on stone anvils to break nuts that are harder and smaller. However, in one population they use an additional stone to increase the stability of the stone or to level the stone anvil (Matsuzawa & Yamakoshi, 1996). Similarly, Hunt and Gray (2003) hypothesized that the diversification of *Pandanus* tool designs they found in New Caledonian crows evolved from cumulative changes to earlier versions and hence was the first indication of rudimentary cumulative cultural evolution in a non-human species. Thus, whether cumulative culture is unique to humans is therefore debated, but it is nonetheless clear that humans use many more technologies or behavioral strategies that are beyond the innovation reach of individuals of great apes, and have done so for at least 1.6 million years, with the onset of the Acheulean tool cultures (Klein, 1999).

Possible, non-mutually exclusive explanations for a lack of cumulative culture are (1) the absence of the ability to faithfully acquire novel alternatives, (2) the inability to recognize alternatives as superior and thus flexibly switch to them, and (3) the absence of the ability to produce such superior innovations in the first place. First, Tomasello et al. (1993) stated that cumulative cultural evolution critically depends on innovation and imitation, and perhaps teaching, and that it can not arise by other forms of social learning such as emulation, nor by any form of individual learning alone. Tomasello et al. (1993) reasoned that if one individual would come up with a more efficient technique, for example of fishing termites, observers would only be able to adopt this improved variant if they were capable of imitation, i.e. faithful copying of the actions involved, because in the absence of the imitation ability other individuals would basically have to invent the novel technique independently. At that time, the consensus was that great apes did not have this ability (cf. Tomasello, 2001). However, the capacity for imitation in chimpanzees has been demonstrated more adequately since then (Hopper et al., 2007; Horner & Whiten, 2005; Whiten, 2005; Whiten et al., 2003; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). There are experimental data on orangutans suggesting they can imitate too (Bering, Bjorklund, & Ragan, 2000; Bjorklund, Bering, & Ragan, 2000; Stoinski & Whiten, 2003; Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). An inability of faithful copying thus no longer qualifies as a valid reason for a lack of cumulative culture in apes.

Teaching, the second form of social learning Tomasello et al. (1993) considered to allow cumulative cultural evolution, is not a uniquely human faculty. There is indeed only scant evidence for teaching in great apes (Whiten, 1989). Teaching is clearly present in other taxa (Hoppitt et al., 2008), but is unlikely to represent intentional teaching, sensu Caro and Hauser (1992), and cumulative culture almost inevitably requires intentional teaching. However, teaching may not have been as prominent in pre-agricultural human life, as only little overt teaching was found to occur in a traditional African society (Whiten & Milner, 1984) and among hunter-gatherer societies (Hewlett & Cavalli-Sforza, 1986) who nonetheless clearly do have cumulative forms of culture. Regardless, teaching is only relevant to the spread of cumulatively built-up innovations, not to their origin. Thus, at present there is no consensus about the importance of imitation and teaching as a prerequisite for cumulative cultural evolution (Boyd & Richerson, 1996; Caldwell & Millen, 2008; Heyes, 1993; Laland, 2004; Laland & Hoppitt, 2003; Tomasello et al., 1993).

As to the second reason, Laland (2004) suggested that cumulative culture is made possible by the ability to assess whether a novel solution to a problem yields a higher return than does an established behavior. In essence, this criterion amounts to whether an animal can recognize an innovation and the relative effectiveness of behavioral alternatives, and then switch to the better variant. In an experiment with chimpanzees, Marshall-Pescini & Whiten (2008) found that chimpanzees having learned a first solution did not switch to a more productive alternative that was demonstrated to them. In another experiment, chimpanzees similarly did not even switch to a more productive alternative used by others in the same group when their own technique was made impossible (Hrubesch, Preuschoft, & van Schaik, 2009). Thus, a lack of recognizing superior alternatives and/or of flexibility to switch to them seems to be a promising candidate for explaining the lack of cumulative build-up of techniques in chimpanzees.

The third possible reason for the absence of cumulative culture is that, if observers have trouble recognizing the utility of an innovation, the same may hold true for the inventors themselves. Numerous innovations have been documented for great apes (van Schaik, van Noordwijk, & Wich, 2006; Whiten et al., 1999), but few of them actually represent superior alternatives to a habitual behavior pattern found elsewhere, or if they do, they have been argued to represent innovations roughly all individuals could have invented on their own if all of the external and internal conditions were right (Tennie et al., 2009).

Therefore the ability to produce superior alternatives might be limited in apes, at least as documented in wild populations to date.

The second and third obstacles both refer to a cognitive deficit pointing to a lack of flexibility. Flexibility is considered the hallmark of complex cognitive adaptations for tool use (Chappell & Kacelnik, 2002). In the tool-use context, flexibility is expressed in the ability to select an appropriate tool for a task. For instance, Chappell & Kacelnik (2002) showed that New Caledonian crows were able to select a stick matching the distance to the target. Similarly, Fox et al. (1999) showed that Sumatran orangutans selected tools of varying dimensions depending on detailed features of the task. But flexibility is more often expressed as producing an appropriate response when conditions have changed (e.g. Lefebvre, Whittle, Lascaris, & Finkelstein, 1997; Piersma & Drent, 2003; Sol & Lefebvre, 2000; Sol, Lefebvre, & Rodriguez-Teijeiro, 2005). Behavioral flexibility (sometimes also called behavioral plasticity) has been described as the tendency to use novel means to adjust to environmental change (Lefebvre et al., 1997), or as the ability of individuals to express "distinct behaviors in different contexts through innovation and learning processes" (Sol et al., 2005). Species and populations with high behavioral flexibility are expected to be characterized by a high innovation frequency (Reader & Macdonald, 2003). Innovation is one component of behavioral flexibility, but the tendency for social learning and to use tools have also been considered components of behavioral flexibility (Reader & Laland, 2002). The concept of flexibility comes very close to that of intelligence (Byrne, 1995).

In sum, behavioral flexibility includes both the ability to innovate, as well as the ability to switch to another solution if appropriate (and thus recognizing its utility). We therefore use and define behavioral flexibility as individuals' continued interest in and acquisition of new solutions to a task, through either innovation or social learning, after already having mastered a previous solution. This behavioral flexibility is a vital precondition for cumulative build-up of techniques, and eventually for cumulative culture. As novel conditions arise, behavioral flexibility may be expressed as innovations that represent solutions that cumulatively build upon ("ratchet") previous ones.

Accordingly, the objectives of this study of captive orangutans were to investigate (1) their behavioral flexibility, i.e. their tendency to switch to other techniques when advantageous or necessary, and (2) their ability to show cumulative build-up of techniques as conditions are changing.

The first objective was to investigate whether captive orangutans satisfy the vital prerequisite for cumulative culture of behavioral flexibility by showing sustained acquisition of new solutions to a problem-solving task. We examined whether subjects would switch techniques, and thus relinquish established techniques, if this was advantageous to them, either because another technique was more efficient, or because the established technique has been made impossible by changing conditions of the task; or whether they would instead be conservative in the techniques they apply and would stick to an initially learned or established technique, as has been found for chimpanzees (Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008). We therefore initially provided a task under the regular condition that gave rise to potentially more solutions than were later possible under restricted conditions. If subjects behave flexibly, we expect them to switch techniques once their original technique was no longer possible. We also examined whether subjects improved gradually in selecting techniques that were not merely appropriate to solve the task, but also more efficient.

The second objective was to investigate whether the captive orangutans show cumulative build-up of techniques, as conditions of the task changed. The experimental setup to test for the subjects' behavioral flexibility was also designed to potentially lead to solutions cumulatively building up on previous ones. Tomasello et al. (1993) recognize cumulative cultural evolution when members of a cultural group acquire a practice begun by others relatively faithfully, and then modify it as needed to deal with novel exigencies, which is again acquired by others. Novel exigencies, or changing conditions, are thus part of this description of cumulative culture, suggesting that without such novel exigencies there would be no cumulative build-up of techniques. (Note, however, that a more demanding level of cumulative culture could potentially be based on cumulative change under constant conditions).

Methods

Animals and living conditions

The study was conducted in Zurich Zoo. Subjects were not deprived of food or water. The zoo population consisted of 9 Sumatran orangutans, 7 females (ages: Lea 40 (did not participate); Timor 32; Selatan 24; Oceh 19; Tuah 14; Xirah 10; Cahaya 5) and 2 males (ages: Djarius 13; Dahulu 4 (the latter excluded from examination due to young age)). For examination we could therefore use seven subjects. The orangutans were socially housed in one main indoor cage (480 m^3), an adjacent smaller indoor cage (192 m^3) and an outdoor cage (188 m^3). They also had the possibility to retreat in boxes formerly used as sleeping boxes. The cages were equipped with tree trunks and ropes, which allowed the animals to show their natural locomotion, and a water source; an environmental enrichment program was provided almost daily.

Apparatus

The task was inspired by the challenge of acquiring water from a deep tree hole in the wild. Wild orangutans have been observed to use two innovative behaviors to get to water in this context: "Branch scoop" (using leafy branch to dip in water) and "Sponging" (absorb water with crumpled leafs) (van Schaik et al., 2006). To transfer this task into an experimental setup in captivity, we used two transparent tubes that were maximally one quarter full with syrup. Two types of tubes were used: Both were 35 cm in height, but they differed in their inner diameter, which was either 10 cm or 5 cm. The wide tube allowed all animals to reach about 20 cm into the tube with their hands, except for the adult male (whose hands were too large). In contrast, the narrower tube did not allow subjects to reach inside with their hand (except for the 4 year old youngster who was excluded from the analyses).

Procedure

Experiments were performed at the main indoor cage and orangutans were tested as a group. Two tubes of the same type were attached to the outside of the main cage, at a distance of approximately 2 meters from each other. Subjects could reach with their arms through the grid of the cage to interact with the tubes. Experimental sessions usually lasted 90 minutes; maximally two sessions were run per week. For an overview of the experimental procedure see Table 1. The experiment consisted of the following three phases:

1) Regular condition (REG): First, under the regular condition we used the wide tubes where animals could reach inside with their hands. We expected some of the orangutans' solutions to take advantage of the possibility to reach about halfway inside the tube with the hand. Subjects were provisioned with sticks, leafy twigs, wood wool and paper. Seven sessions of 90 minutes each were performed.

2) Restricted condition 1 (RC1): Second, under the "restricted condition 1" we used the narrower tubes, where animals could no longer reach inside with their hands, to test subjects' behavioral flexibility (objective 1). Hence, the number of possible techniques was restricted to techniques that did not involve reaching partly inside the tube with the hand. Seven sessions under the restricted condition were performed following the last session under the regular condition, the first one lasting only 40 minutes (due to problems with fixing the tubes to the cage), the other six 90 minutes each. We investigated the behavioral response of subjects whose preferred techniques of the regular condition were inhibited under the "restricted condition 1". We aimed at examining whether they would quickly reduce the application of those techniques that no longer yielded a return and switch to different, functional and efficient techniques.

3) Restricted condition 2 (RC2): To test for cumulative build-up of techniques under changing conditions (objective 2), the experiment under the restricted condition was continued, but at the 8^{th} session we added a further restriction by removing the supply of leafy twigs, inhibiting the "Branch scoop" behavior known from the wild. This new condition served to suppress the hitherto favorite techniques. Another seven sessions of 90 minutes each were performed, for a total of 14 sessions with the narrower tube. By inhibiting preferred efficient techniques we intended to keep subjects' motivation high to acquire new solutions, which might potentially lead to cumulative build-up of techniques.

Criteria of cumulatively built-up techniques

We used the following criteria for innovative techniques to qualify as cumulatively building up on previous techniques, and thus allow cumulative culture. First, the new technique is more complex (Boesch & Tomasello, 1998; Tomasello et al., 1993), i.e. its range of application is larger (Boesch & Tomasello, 1998), the number of physically distinct constituent components (also called "technounits") is higher (Oswalt, 1976), or the number of behavioral steps involved is higher. Second, the new technique is an elaboration of a previous one, i.e. includes a variation or a behavioral element of a previous one, as suggested by Marshall-Pescini & Whiten (2008). Therefore we only expect individuals that have used the specific component technique(s) to master the corresponding built-up technique. Otherwise the technique does not qualify as cumulatively built-up.

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Behavioral coding

Techniques were categorized based on their efficiency to gain syrup and on the range of conditions under which they worked. Efficiency of a technique depended on the absorptivity of the material used. Techniques that yielded only a low return because the material used absorbs very little fluid (here a bare stick) were assigned as non-efficient techniques. Efficient techniques involved materials that soak up fluids (e.g. paper, wood wool, leaves of a leafy twig). There were techniques that were efficient to acquire syrup in all phases of the experiment; several others were efficient under the regular condition but not possible under restricted conditions 1 and 2; and one technique (Branch scoop) was efficient in REG and RC1 but was made impossible in RC2. An overview of the suitability of the different techniques under the three conditions is provided in Table 1.

Data coding and analyses

The experiments were all recorded with two video cameras, each directed at one tube. Continuous behavior sampling was done from video records. Statistics were calculated in SPSS 14.0. Page's L Trend Test (Page, 1963) was used to test for successive improvement in the use of techniques over the seven sessions under REG and RC1.

Results

All individuals, except the oldest female, participated in the task and actively manipulated the syrup-tubes in all the three conditions for varying, but always substantial, amounts of time. The duration of the three conditions were similar, ranging from 10 to 10.5 hours; given that two tubes were provided this allowed interaction times with a tube summed over all subjects of 20 to 21 hours under all three conditions. The tubes were used by subjects for the majority of the time, but because they remained unoccupied for a sufficiently long part, roughly 7 hours for each of the three conditions, individual access to the task was not limited (Table 2).

Regular Condition: Baseline

Under the regular condition (REG), the first solution to the task for six of seven test subjects was the use of a stick to dip into the syrup-tube and then licking syrup from the stick ("Dip stick"). Five subjects used this technique within the first 15 minutes. It did not yield a high return as sticks hardly absorbed any syrup; hence it was appraised as a non-efficient technique. But already within the first session, the subjects came up with four innovative and efficient techniques, using twigs, paper and wood wool, materials that all soaked up more syrup, and therefore these techniques were more efficient (see Table 3 for a detailed description of all techniques and the latency to first occurrence). Over time, subjects increasingly solved the task by applying efficient techniques (see Table 1 for an overview which techniques were efficient in which phase of the experiment), rather than by the simple but inefficient "Dip stick". Page's L Trend Test (Page, 1963) revealed that there was a highly significant trend for subjects to gradually increase their successful use of efficient techniques, expressed as a proportion of their total manipulation time (L = 873.5; k = 7; n = 7; p < .01).

What kind of techniques did subjects use in phase REG? We determined subjects' most preferred techniques by analyzing their manipulation activities in the last two sessions (in REG) they were actively engaged with the task. Subjects showed substantial variation in their most preferred techniques, with the four most commonly used techniques distributed across seven different individuals (Table 4). One subject (Selatan) preferred to use efficient techniques that would still be possible under the "restricted condition 1" (RC1, the next experimental phase) for most of its manipulation time (Table 4): "Branch scoop" (74.5%), "Twisted paper rod" (21.4%) and "Vegetable rod" (4.1%). Five individuals (Ca, Oc, Ti, Tu, Xi) faced the problem that they almost exclusively preferred to use efficient techniques that had been efficient so far in phase REG but that would no longer be possible in the next experimental phase RC1 ("Paper squash", "Wood wool squash", "Twig squash", "Sponging") with the narrower tube (Table 4). All five animals had used those efficient techniques that would still be possible in phase RC1 (see Table 1) only for less than 3% of their total manipulation time in REG; one had never performed any such technique. These five animals were therefore the focus of the next experimental phase RC1. Would they quickly reduce the application of techniques that no longer work and flexibly switch to other solutions that are efficient?

Objective 1: Flexibility to abandon a non-functional technique and switch to a functional technique

a) Switch 1: Regular condition – restricted condition 1. During RC1 (restricted condition 1), the tubes were made 5 cm narrower. One subject (Selatan) under REG exclusively preferred efficient techniques that would still work with the narrower tube, and she kept on applying these techniques in RC1. Five subjects (Ca, Oc, Ti, Tu, Xi) had preferentially used efficient techniques during REG that were no longer possible in RC1, with the narrower tube (Figure 1a: left half: dashed line). These five subjects largely still tried to apply them in vain in the first RC1 session, but then gradually reduced the proportion of their manipulation time dedicated to these now ineffective techniques, and after the fourth session these techniques had almost completely been abandoned (Figure 1a: right half: dashed line). Page's L Trend Test revealed that subjects highly significantly reduced applying these techniques over the seven sessions under the "restricted condition 1" ($L = 660$; $k = 7$; $n = 5$; $p < .001$).

As they reduced applying previously efficient techniques, they could either have gone back using the non-efficient technique "Dip stick" all but one of them had used initially under the regular condition (which would still work), or they could have switched to efficient techniques they had used only very rarely in REG (totaling 0-3% of their manipulation time) or had not learned yet at all. Indeed, initially they all relied on the non-efficient technique "Dip stick" to gain syrup, averaging 77.4 % of their successful manipulation time in the first two sessions of RC1, but they more and more started using techniques that were efficient in RC1 (Figure 1a: right half: bold line; see Table 1 for efficient techniques in RC1). Page's L Trend Test revealed a highly significant trend of subjects gradually increasing successful use of techniques efficient in RC1 as a proportion of their total manipulation time (L = 622.5; k = 7; n = 5; p < .01). So finally, all five animals that had been forced to abandon their hitherto preferred techniques successfully did so and switched to techniques that were functional and efficient under RC1 (Figure 1a). For the whole study group the preference for these efficient techniques was significantly greater in RC1 than in REG (Wilcoxon signed-ranks test: Z = -2.023; n = 7; p = .043). Thus, despite some initial reluctance, the orangutans in this study were able to switch to new techniques when their preferred old technique was made impossible.

b) Switch 2: Restricted condition 1 – restricted condition 2. In the last two sessions of RC1, four subjects (Sel, Ti, Tu, Xi) used the "Branch Scoop" technique for an average of 75.2% of their manipulation time (Figure 1b: left half: dashed line). Under RC2 (restricted condition 2), the supply with leafy twigs was terminated to inhibit the "Branch Scoop" technique. These four individuals had to abandon their preferred technique, three of them (Ti, Tu, Xi) for the second time. They were forced to use techniques in RC2 (see Table 1 for efficient techniques in RC2) they had not used much in RC1 (totaling 3-21% of their manipulation time), or not learned yet at all. Subjects again demonstrated high behavioral flexibility by abandoning a preferred technique (Branch scoop) and successfully switching to different efficient techniques (Figure 1b). For the whole study group the preference for efficient techniques other than "Branch Scoop" was significantly greater in RC2 than RC1 (Wilcoxon signed-ranks test: Z = -2.023; n = 7; p = .043).

Objective 2: Cumulative build-up of techniques?

During restricted conditions, two solutions eventually emerged that fulfilled the criteria of a cumulatively built-up (ratcheted) technique: the "Squash-and-fish" technique and the "Drop-and-fish" technique.

The "Squash-and-fish" technique builds up on the techniques "Paper-squash" and "Fish" (see Table 3 for definitions) and was first invented by one animal (Ti) in the last session of RC1, i.e. after more than 19 hours of experimentation. In "Squash-and-fish" a subject uses a stick to push some paper down the tube into the syrup. After the paper had soaked up syrup, the subject removed it by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards. The "Squash-and-fish" technique fully meets our two criteria for a ratcheted technique. First, it is more complex than "Paper-squash" for two reasons: it involves an additional component (the stick), and it can be applied in a greater number of situations, namely with both the wide and the narrow tube. Second, it represents an elaboration of the previous technique "Paper-squash", as the stick substitutes for hand and arm. The progress on the technique "Fish" is also obvious. When applying the technique "Fish," a subject took out any objects that had happened to fall into the syrup before through somebody's actions. In contrast, with "Squash-and-fish" a piece of paper or wood wool was put into the syrup and then immediately afterwards taken out again by the same single individual. The techniques "Paper-squash" and "Fish" are both clearly pre-stage techniques of "Squash-and-fish", as only subjects that first used both these component techniques (Ca, Ti, Tu) later performed the final ratcheted technique "Squash-

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and-fish" (Figure 2a; Fisher exact test: n = 7; p = .029). No subject directly learned the technique "Squash-and-fish" without having learned "Paper-squash" and "Fish" before.

The second ratcheted technique they invented is "Drop-and-fish". It builds up on the techniques "Sponging" and "Fish" (see Table 3 for definitions) and was first discovered by a subject (Tu) in the first session of RC2, i.e. after more than 20 hours of experimentation. In "Drop-and-fish", paper or wood wool chewed to a ball is dropped into the syrup; after that ball had soaked up syrup the subject would take it out by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards. "Sponging" and "Fish" are obviously pre-stage techniques of "Drop-and-fish", as only subjects that first used both these component techniques (Ca, Ti, Tu, Xi) later performed the final ratcheted technique "Drop-and-fish" (Figure 2b; Fisher exact test: n = 7; p = .029). Subjects had to know both component techniques to master the ratcheted technique.

Discussion

Behavioral flexibility (objective 1)

This study first demonstrated that captive orangutans of Zurich Zoo complied with the vital prerequisite for cumulative culture of behavioral flexibility by showing continued interest in acquiring new solutions to a problem-solving task, and furthermore by switching to other techniques and relinquishing established techniques when this was advantageous.

Even under the regular condition, subjects kept exploring the problem and acquiring new solutions despite having mastered an initial technique. Most subjects started with a non-efficient technique ("Dip stick"), but then spontaneously came up with innovative and more efficient solutions, and eventually largely switched to these and preferentially used them. Minimally, this indicates that they recognized which of two techniques yields a higher return, which has been suggested as a prerequisite for cumulative culture (Laland, 2004; Marshall-Pescini & Whiten, 2008). At the same time, most individuals kept on using a variety of techniques under the regular condition, predicting they would show high flexibility to abandon preferred techniques and switch to different techniques as the condition was changed. Moreover, subjects showed great diversity in their most preferred techniques (with the four different most preferred techniques distributed across seven different individuals) which would not be expected if subjects followed rules of conformity (Henrich & Boyd, 1998), where they had ended up with one technique being preferred in the group. We return to this topic below.

As the condition was restricted a first time by narrowing the tube, those five subjects whose preferred efficient techniques had thereby been made impossible, initially still unsuccessfully tried to apply them. Conservative subjects (cf. Hrubesch et al., 2009) would continue to do so for a long time. But the orangutans in this study gradually reduced the proportion of manipulation time dedicated to vainly apply their preferred techniques that no longer yielded a return. Instead, they first switched back to the non-efficient technique "Dip stick" that all but one of them had used initially under the regular condition, but eventually they began to switch to more efficient techniques. We found that these subjects in the "restricted condition 1" (RC1) significantly increased the use of different techniques that were functional and efficient but that they had hardly ever used before (in the regular condition less than 3% of their total manipulation time) or not known at all, revealing a high level of behavioral flexibility.

As the condition was restricted a second time by removing all leafy twigs, the "Branch scoop" technique that had become the preferred technique of four individuals was made impossible. Subjects again demonstrated a high flexibility to abandon a preferred technique that had been made non-functional and to switch successfully to different, functional and efficient techniques.

Such flexible switching of techniques contrasts with the findings of chimpanzees in similar situations, where several studies report them to show a bias of conformity or conservatism (Bonnie, Horner, Whiten, & de Waal, 2007; Hrubesch et al., 2009; Marshall-Pescini & Whiten, 2008; Whiten, Horner, & de Waal, 2005). Conformity implies that individuals possess a propensity to preferentially adopt the solution being most common in the population, thus eventually leading to the same solution to a problem in the whole population (Henrich & Boyd, 1998). In a task where two different techniques were possible solutions, a substantial number of chimpanzees able to use both methods adopted the group's norm, thus perhaps showing a conformity bias (Whiten et al., 2005). For the present purpose, it is irrelevant whether the chimpanzees showed true conformity in the sense of positive, frequency-dependent social leaning where the probability of acquiring a trait increases disproportionately with the number of demonstrators performing it (Boyd & Richerson, 1985).

Alternatively, conservatism implies that individuals that had become proficient with a first technique did not switch to the second one that was considered more efficient, not even after the first technique had been made ineffective (Hrubesch et al., 2009). Thus, having learned a particular solution suppresses further exploration of the task and thus prevents the emergence of other solutions (Boyd & Richerson, 1985). Interestingly, Marshall-Pescini & Whiten (2008) also found that chimpanzees who had acquired a first solution to a task did not learn a second, more complex and productive solution that incorporated the core actions of the first technique. They concluded their chimpanzees to have become "stuck" on a technique they had learned initially, inhibiting cumulative social learning and possibly constraining the species' capacity for cumulative cultural evolution.

Whether these chimpanzees showed conservatism or conformity, they showed very limited behavioral flexibility. However, for a proper comparison of the behavioral flexibility of orangutans and chimpanzees, the same experiments would have to be conducted in multiple groups of both.

Cumulative build-up of techniques (objective 2)

Second, this study demonstrated that captive orangutans were capable of cumulative build-up on previous techniques as conditions of the task changed. These ratcheted techniques were then also adopted by some other group members, suggesting that modest cumulative culture could actually be possible in captive orangutans, at least if they have to deal with novel conditions.

As we restricted conditions of the task, first by using a narrower tube, and second by ceasing to supply the animals with leafy twigs, we inhibited most of the efficient techniques used preferentially under the regular condition. This kept subjects' motivation high to invent and acquire new solutions, as they were very eager to get syrup. Indeed, they eventually came up with two solutions that fulfilled the criteria of a ratcheted technique (and that would allow cumulative culture). These techniques were more complex and they were performed only by subjects that had mastered the pre-stage techniques previously.

Finally, although it was not within the scope of this study to study social learning, to amount to cumulative culture the ratcheted techniques would have to be adopted by other group members (Boesch & Tomasello, 1998). Indeed, in our group the two ratcheted techniques "Squash-and-fish" and "Drop-and-fish" were performed by three and four subjects, respectively. Subjects that acquired such a technique, after a first individual invented them, previously observed the performance of the new technique, suggesting they used this social information to adopt the ratcheted techniques by socially mediated learning, establishing a cumulative tradition.

Novel exigencies, or changing conditions, are part of Tomasello et al.'s (1993) description of cumulative culture, which suggests that without such novel exigencies there would be no cumulative build-up of techniques. In our present study, we created novel exigencies by changing conditions of the task. Indeed, this was probably crucial for the invention of the two ratcheted techniques. Although subjects showed exploration during the regular condition, the invention of these ratcheted techniques was clearly stimulated by the inhibition of previous solutions. This could explain why cumulative build-up of techniques was possible in this set-up and a cumulative tradition was established in the present group of captive orangutans.

From the wild, there are no similar observations of cumulative build-up of techniques in orangutans up to date. They largely seem to fail to produce superior innovations in the first place. Indeed, captive and ex-captive rehabilitant orangutans have been found to be far more innovative than wild ones (Lehner, Burkart, & van Schaik, 2010; Russon, Kuncoro, Ferisa, & Handayani, 2010; Russon et al., 2009). Lehner et al. (2010) suggested that captive orangutans associate novelty with the presence of food rewards, thus favoring the appearance of innovations and, given excellent conditions for social transmission, their retention. This leads to larger innovation repertoires in captive populations compared to wild ones. Consequently, cumulative build-up of techniques can be expected to occur in captive orangutans more likely than in wild conspecifics as well.

Given this contrast between captive and wild subjects, it would be interesting to introduce our present experiment into a wild population of orangutans. We would first choose a population where orangutans have been observed by van Schaik et al. (2006) to use the techniques "Branch scoop" (in Suaq Balimbing on Sumatra) or "Sponging" (Ketambe, Sumatra) to collect water from a deep tree hole. Supposing they would voluntarily approach and engage with the set-up we could eventually compare their performance with the captive subjects. Potentially, this might lead to the foundation of the same cumulative tradition in wild orangutans too.

Our findings suggested that creating novel exigencies by inhibiting preferred techniques was crucial to motivate subjects to modify and improve on present solutions. We will address this possible influence of novel exigencies in a subsequent experiment with our group of captive orangutans of Zurich Zoo. A more stringent test for a population's potential for cumulative culture would be to investigate the ability for cumulative build-up of techniques under constant conditions. Nevertheless the results presented here showed that cumulative build-up of techniques is not per se a uniquely human characteristic, because two ratcheted techniques were invented by the orangutans of Zurich Zoo. This suggests that modest cumulative culture could be possible in captive orangutans, at least when they have to deal with novel exigencies.

References

Bering, J. M., Bjorklund, D. F., & Ragan, P. (2000). Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Developmental Psychobiology, 36*(3), 218-232.

Bjorklund, D. F., Bering, J. M., & Ragan, P. (2000). A two-year longitudinal study of deferred imitation of object manipulation in a juvenile chimpanzee (Pan troglodytes) and orangutan (Pongo pygmaeus). *Developmental Psychobiology, 37*(4), 229-237.

Boesch, C. (1996). The emergence of cultures among wild chimpanzees. In W. G. Runciman, J. Maynard-Smith & R. I. M. Dunbar (Eds.), *Evolution of social behaviour patterns in monkeys and man* (pp. 251-268). London: British Academy.

Boesch, C. (2003). Is culture a golden barrier between human and chimpanzee? *Evolutionary Anthropology, 12*(2), 82-91.

Boesch, C., & Tomasello, M. (1998). Chimpanzee and human cultures. *Current Anthropology, 39*(5), 591-614.

Bonnie, K. E., Horner, V., Whiten, A., & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B-Biological Sciences, 274*(1608), 367-372.

Boyd, R., & Richerson, P. J. (1985). *Culture and the evolutionary process.* Chicago: University of Chicago Press.

Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. In W. G. Runciman, J. Maynard-Smith & R. I. M. Dunbar (Eds.), *Evolution of social behaviour patterns in monkeys and man* (pp. 77-93). Oxford: Oxford University Press.

Byrne, R. W. (1995). *The thinking ape: Evolutionary origins of intelligence*. Oxford: Oxford University Press.

Byrne, R. W. (2007). Culture in great apes: using intricate complexity in feeding skills to trace the evolutionary origin of human technical prowess. *Philosophical Transactions of the Royal Society B-Biological Sciences, 362*(1480), 577-585.

Caldwell, C. A., & Millen, A. E. (2008). Studying cumulative cultural evolution in the laboratory. *Philosophical Transactions of the Royal Society B-Biological Sciences, 363*(1509), 3529-3539.

Caro, T. M., & Hauser, M. D. (1992). Is There Teaching in Nonhuman Animals. *Quarterly Review of Biology, 67*(2), 151-174.

Chappell, J., & Kacelnik, A. (2002). Tool selectivity in a non-primate, the New Caledonian crow (Corvus moneduloides). *Animal Cognition, 5*(2), 71-78.

Lehner, S. R., Burkart, J. M. & van Schaik, C. P. 2011: Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques? J. Comp. Psychol. **125**, 446-455. (doi:10.1037/a0024413).

Fox, E. A., Sitompul, A. F., & van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell & H. L. Miles (Eds.), *The mentalities of gorillas and orangutans* (pp. 99-116). Cambridge: Cambridge University Press.

Henrich, J., & Boyd, R. (1998). The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior, 19*(4), 215-241.

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology, 12*(3), 123-135.

Hewlett, B., & Cavalli-Sforza, L. L. (1986). Cultural transmission among Aka pygmies. *American Anthropologist, 88*, 922-934.

Heyes, C. M. (1993). Imitation, Culture and Cognition. *Animal Behaviour, 46*(5), 999-1010.

Hopper, L. M., Spiteri, A., Lambeth, S. P., Schapiro, S. J., Horner, V., & Whiten, A. (2007). Experimental studies of traditions and underlying transmission processes in chimpanzees. *Animal Behaviour, 73*, 1021-1032.

Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., et al. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution, 23*(9), 486-493.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (Pan trogiodytes) and children (Homo sapiens). *Animal Cognition, 8*(3), 164-181.

Hrubesch, C., Preuschoft, S., & van Schaik, C. (2009). Skill mastery inhibits adoption of observed alternative solutions among chimpanzees (Pan troglodytes). *Animal Cognition, 12*(2), 209-216.

Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society of London Series B-Biological Sciences, 270*(1517), 867-874.

Klein, R. G. (1999). *The human career: human biological and cultural origins* (2 ed.). Chicago: University of Chicago Press.

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32*(1), 4-14.

Laland, K. N., & Hoppitt, W. (2003). Do animals have culture? *Evolutionary Anthropology, 12*(3), 150-159.

Lefebvre, L., Whittle, P., Lascaris, E., & Finkelstein, A. (1997). Feeding innovations and forebrain size in birds. *Animal Behaviour, 53*, 549-560.

Lehner, S. R., Burkart, J. M., & van Schaik, C. P. (2010). An evaluation of the geographic method for recognizing innovations in nature, using zoo orangutans. *Primates, 51*(2), 101-118.

Marshall-Pescini, S., & Whiten, A. (2008). Chimpanzees (Pan troglodytes) and the question of cumulative culture: an experimental approach. *Animal Cognition, 11*(3), 449-456.

Matsuzawa, T., & Yamakoshi, G. (1996). Comparison of chimpanzee material culture between Bossou and Nimba, West Africa. In A. E. Russon, K. A. Bard & S. T. Parker (Eds.), *Reaching into thought* (pp. 211-232). Cambridge: Cambridge University Press.

Oswalt, W. H. (1976). *An anthropological analysis of food-getting technology.* New York: John Wiley.

Page, E. B. (1963). Ordered hypotheses for multiple treatments - a significance test for linear ranks. *Journal of the American Statistical Association, 58*(301), 216-230.

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution, 18*(5), 228-233.

Reader, S. M., & Laland, K. N. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America, 99*(7), 4436-4441.

Reader, S. M., & Macdonald, K. (2003). Environmental variability and primate behavioural flexibility. In S. M. Reader & K. N. Laland (Eds.), *Animal Innovation* (pp. 83-116). Oxford: Oxford University Press.

Russon, A. E., Kuncoro, P., Ferisa, A., & Handayani, D. P. (2010). How Orangutans (Pongo pygmaeus) Innovate for Water. *Journal of Comparative Psychology, 124*(1), 14-28.

Russon, A. E., van Schaik, C. P., Kuncoro, P., Ferisa, A., Handayani, D. P., & Van Noordwijk, M. A. (2009). Innovations and intelligence in orangutans. In S. A. Wich, S. S. Utami Atmoko, T. Mitra Setia & C. P. van Schaik (Eds.), *Orangutans: Geographic variation in behavioral ecology and conservation* (pp. 279-298): Oxford University Press.

Lehner, S. R., Burkart, J. M. & van Schaik, C. P. 2011: Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques? J. Comp. Psychol. **125**, 446-455. (doi:10.1037/a0024413).

Sol, D., & Lefebvre, L. (2000). Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos, 90*(3), 599-605.

Sol, D., Lefebvre, L., & Rodriguez-Teijeiro, J. D. (2005). Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. *Proceedings of the Royal Society B-Biological Sciences, 272*(1571), 1433-1441.

Stoinski, T. S., & Whiten, A. (2003). Social learning by orangutans (Pongo abelii and Pongo pygmaeus) in a simulated food-processing task. *Journal of Comparative Psychology, 117*(3), 272-282.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: on the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B-Biological Sciences, 364*(1528), 2405-2415.

Tomasello, M. (2001). Cultural transmission - A view from chimpanzees and human infants. *Journal of Cross-Cultural Psychology, 32*(2), 135-146.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural Learning. *Behavioral and Brain Sciences, 16*(3), 495-511.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., et al. (2003). Orangutan cultures and the evolution of material culture. *Science, 299*(5603), 102-105.

van Schaik, C. P., van Noordwijk, M. A., & Wich, S. A. (2006). Innovation in wild Bornean orangutans (Pongo pygmaeus wurmbii). *Behaviour, 143*, 839-876.

Whiten, A. (1989). Parental encouragement in *Gorilla* in comparative perspective: implications for social cognition. In S. T. Parker, H. L. Miles & R. W. Mitchell (Eds.), *The mentality of gorillas and orangutans* (pp. 342-366). Cambridge: Cambridge University Press.

Whiten, A. (2005). The second inheritance system of chimpanzees and humans. *Nature, 437*(7055), 52-55.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., et al. (1999). Cultures in chimpanzees. *Nature, 399*(6737), 682-685.

Whiten, A., Horner, I., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning & Behavior, 32*(1), 36-52.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature, 437*(7059), 737-740.

Whiten, A., Horner, V., & Marshall-Pescini, S. (2003). Cultural panthropology. *Evolutionary Anthropology, 12*(2), 92-105.

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society B-Biological Sciences, 364*(1528), 2417-2428.

Whiten, A., & Milner, P. (1984). The educational experiences of Nigerian infants. In H. V. Curran (Ed.), *Nigerian children: developmental perspectives* (pp. 34-73). London: Routledge and Kegan Paul.

Lehner, S. R., Burkart, J. M. & van Schaik, C. P. 2011: Can captive orangutans (Pongo pygmaeus abelii) be coaxed into cumulative build-up of techniques? J. Comp. Psychol. **125**, 446-455. (doi:10.1037/a0024413).

Table 1
Experimental setup

Task	Regular condition	Restricted condition 1	Restricted condition 2
Tube diameter	10 cm	5 cm	5 cm
Sticks, wood wool, paper	Yes	Yes	Yes
Leafy twigs	Yes	Yes	No
Duration	7 sessions of 90 min	1 session of 40 min, 6 sessions of 90 min	7 sessions of 90 min
Techniques	**Regular condition**	**Restricted condition 1**	**Restricted condition 2**
Efficient techniques shown	Branch Scoop, Fish, Twisted paper rod, Vegetable rod, Paper squash, Wood wool squash, Twig squash, Sponging	Branch Scoop, Fish, Twisted paper rod, Vegetable rod, Squash-and-fish	Fish, Twisted paper rod, Vegetable rod, Squash-and-fish, Drop-and-fish
Non-efficient techniques	Dip stick	Dip stick	Dip stick
Impossible techniques		Paper squash, Wood wool squash, Twig squash, Sponging	Branch scoop, Paper squash, Wood wool squash, Twig squash, Sponging

Note. The experiment consisted of three phases: (1) Regular condition, (2) restricted condition 1, where the tube was narrowed, and (3) restricted condition 2, where the supply with leafy twigs was stopped. Table explicitly states for every phase of the experiment which of the shown techniques were efficient, inefficient, or made impossible.

Table 2
Individuals' participation in the task under the three different conditions

Individual	Regular condition	Restricted condition 1	Restricted condition 2
Ca	00:55:12	01:22:06	02:07:34
Dj	00:08:44	00:07:00	00:02:47
Oc	04:12:55	03:35:14	04:48:31
Sel	03:35:09	03:06:59	02:46:49
Ti	00:31:59	00:27:25	00:19:12
Tu	02:34:22	03:19:45	04:00:40
Xi	00:42:01	00:46:52	00:15:08
None	07:08:30	07:01:00	07:14:30

Note. Participation is presented as duration (hh:mm:ss) of active manipulation with the tubes for each subject and condition. The last line indicates for how long either of the two tubes was not used by any subject.

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Table 3

Techniques used to solve the syrup-tube task

Behavior	Description	Latency
Dip stick	Dip a bare stick into the tube, then lick the syrup from the stick	00:00:50
Paper squash	Force paper directly with hand into the tube, pull paper out, take it in mouth and suck it	00:39:15
Wood wool squash	Force wood wool directly with hand down into the tube, pull wood wool out, take it in mouth and suck it	00:40:15
Twig squash	Squash twig into the tube with hand reaching inside the tube, then pull twig out and suck it	04:33:00
Sponging	Paper or wood wool chewed to a ball is dropped inside the tube; then reach with hand down into the syrup, take it out by hand, take the whole piece into the mouth, chew and suck it (like chewing gum)	01:44:00
Branch scoop	Use a twig with leaves like a rod, so hand is only slightly or not at all inside the tube; pull twig out, then suck syrup out by gently chewing the leaves	00:12:30
Fish	Use a stick to get out leaves, paper or wood wool that have accrued in the tube by simultaneously pushing such an item with the stick against the inner wall of the tube and lifting the stick upwards	00:11:17
Twisted paper rod (TPR)	Twist paper and use it as a rod by holding one end down in the syrup, pulling it out, and sucking it	09:59:00
Vegetable rod	Use vegetables like leek or chard as a rod by holding it down in the syrup, pulling it out, and sucking it	02:46:00
Squash-and-fish	Use a stick to force paper down into the syrup; get paper out by simultaneously pushing the paper with the stick against the inner wall of the tube and pulling the stick upwards	19:21:00
Drop-and-fish	Paper or wood wool chewed to a ball is dropped inside the tube; get it out by simultaneously pushing the paper ball with a stick against the inner wall of the tube and pulling the stick upwards	20:23:25

Note. Descriptions are given of all techniques the subjects used to solve the syrup-tube task. Additionally, the latency (hh:mm:ss) from the beginning of the experiment till the first occurrence of each technique is given.

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Table 4

Subjects' two favorite techniques used under the regular condition (REG)

Individual	Preferred Technique	% used	2nd preferred Technique	% used
Ca	Wood wool squash (REG)	65.4	Paper squash (REG)	20.3
Dj	Dip stick (inefficient)	100		
Oc	Wood wool squash (REG)	56.4	Paper squash (REG)	19.8
Sel	Branch scoop (REG & RC1)	74.5	Twisted paper rod (REG & RC1)	21.4
Ti	Paper squash (REG)	51.3	Sponging (REG)	43.6
Tu	Paper squash (REG)	74.1	Wood wool squash (REG)	14.5
Xi	Wood wool squash (REG)	59.9	Paper squash (REG)	24.1

Note. Subject's preferred techniques are indicated as percentage of their successful manipulation time in the last two sessions of the regular condition. In brackets it is stated whether a technique was inefficient, efficient in the regular condition only (REG), or if the technique was efficient in the regular condition as well as in the following experimental phase, the restricted condition 1 (REG & RC1).

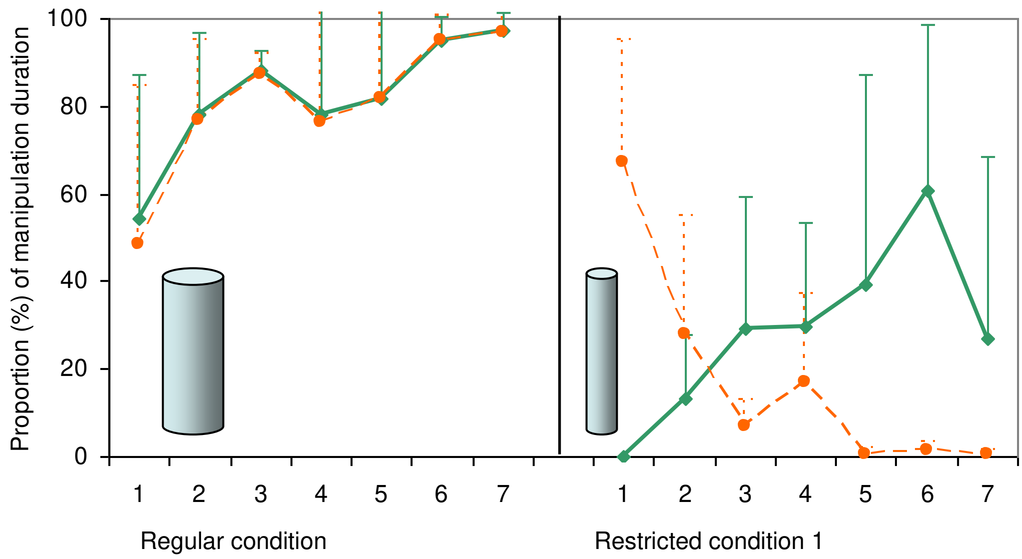

Figure 1a. Behavioral flexibility 1: Regular condition – restricted condition 1:

Bold line: Average proportion of total manipulation time used by subjects (N = 5: Ca, Oc, Ti,Tu, Xi) for performing efficient techniques in the seven sessions under regular condition (REG) and, after novel exigencies had been created by providing a narrower tube, in the seven sessions under restricted condition 1 (RC1).

Dashed line: Average proportion of techniques that were efficient in REG but that had been made impossible in RC1, thus in RC1 indicating how much subjects in vain still tried to apply them.

Means and SD are shown. Flexibility demonstrated by those five subjects forced to abandon their preferred techniques and to switch to different techniques.

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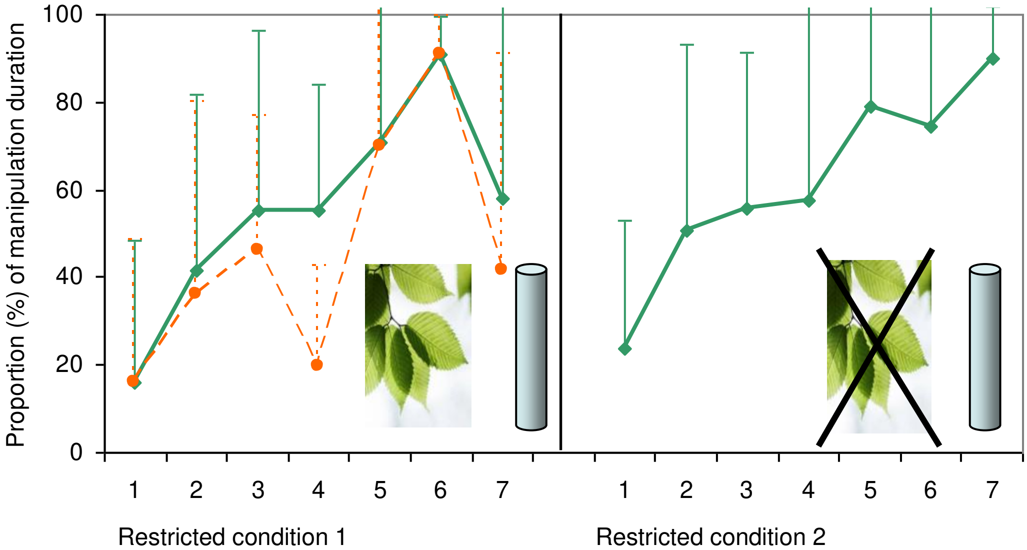

Figure 1b. Behavioral flexibility 2: Restricted condition 1 – restricted condition 2:

Bold line: Average proportion of total manipulation time used by subjects (N = 4: Sel, Ti,Tu, Xi) for performing efficient techniques in the seven sessions under restricted condition 1 (RC1) and, after novel exigencies had been created by terminating the supply with twigs, in the seven sessions under restricted condition 2 (RC2).

Dashed line: Average proportion of technique “Branch scoop” that was efficient in RC1 but impossible in RC2.

Means and SD are shown. Flexibility demonstrated by those four subjects forced to abandon their preferred technique “Branch scoop” and to switch to different techniques.

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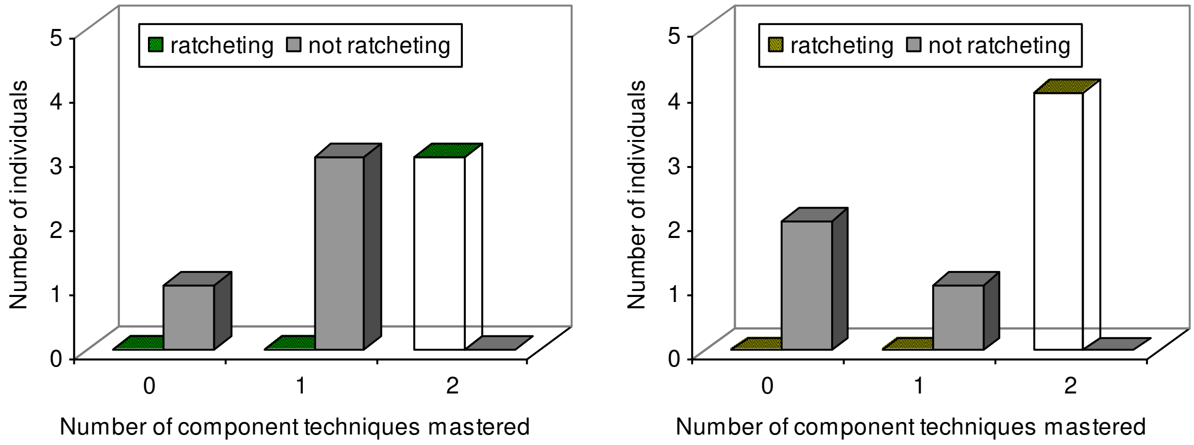

a) Squash-and-fish

b) Drop-and-fish

Figure 2. Cumulative build-up of techniques:
Shows how many individuals succeeded to perform the ratcheted techniques (ratcheting: hatched) and how many failed (not ratcheting: gray), depending on whether they had previously mastered 0, 1, or both its component techniques, for (a) the technique “Squash-and-fish” and (b) the technique “Drop-and-fish”.